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Review

Fossil leaf traits as archives for the past — and lessons for the future?☆

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ABSTRACT

Correlations of leaf traits with environmental conditions are widely used for reconstruction of palaeoclimate and to analyse the evolution of land plants. Evaluation of climate-dependent leaf traits of fossil floras can potentially contribute to our understanding of long-term responses of vegetation to changing climate. In this contribution, basic aspects and methods of palaeoclimate reconstruction by fossil leaf morphology, such as leaf margin analysis and CLAMP, are presented and discussed with respect to recent results on functional leaf traits. Also addressed is the use of stomatal data (density and size) for obtaining palaeoatmospheric CO_2 as well as the (possible) interference of CO_2 with other abiotic environmental parameters, leading to "non-analogue climates" which cannot be found today. There is much evidence that CO_2, as an essential factor for gas exchange and therefore palaeoecophysiology, acted as an important driver in land plant evolution. For instance, elevated CO_2 levels of the past and present are assumed to affect leaf shape evolution, because stomatal conductance is negatively correlated with atmospheric CO_2 thereby affecting leaf heat dissipation. This topic is addressed in detail as an exemplary case of the interference of multiple environmental parameters. Results of a gas exchange model with coupled heat transfer indicate that the effect of elevated CO_2 on leaf temperature may be minor, at least when water supply is not limited. This example demonstrates that ecophysiological analyses of trait–climate relationships can contribute to identifying adaptive features of leaf architecture and to evaluate predictions into the future as well as into the past.

1. Introduction

Leaves as the primary organs of photosynthesis are directly exposed to the atmosphere, performing controlled gas exchange under constantly varying conditions. Successful and economic photosynthesis is a basic necessity of plant life, leading to a high selective pressure on leaf function. Unsurprisingly, leaves are sensitive to their environment in various ways. These comprise instant responses to external stimuli, such as opening or closing of stomata, as well as correlations between macromorphological/micromorphological traits and environmental parameters. Correlations of traits with environment can be interspecific as well as intraspecific, with the latter including leaf plasticity within one individual (for the topic of plasticity, see also Pugielli et al., within this volume). Morphological responses of leaves to environment observed and documented for recent vegetation are the basis for using morphological traits of fossil leaves as "climate archive". By doing so, it is tacitly assumed that correlations between leaf traits and climate have a functional basis that remained constant from the past to the present (Jordan, 2011). If so, then, consequently, these may be extrapolated into the future. Furthermore, evaluation of climate-dependent leaf traits of fossil floras could contribute to our understanding of long-term responses of vegetation to changing climate.

In this contribution, various aspects of climate sensitivity of leaves are considered within the framework of their use as palaeoclimate proxy and related problems of extrapolating extant trait–climate correlations into the past. Although a leaf functional basis is generally assumed for trait–climate correlations, a clear causal explanation is lacking for many of them. Recognizing ecophysiological processes which drive trait–climate correlations is, however, the basis for identifying and explaining adaptations to environment on various levels, from plasticity to evolutionary adaptation and (abiotic) environmental filtering. Therefore, focus will be on traits for which clear physical and physiological explanations for their correlations with environment exist. These are leaf size and its interrelationships with temperature and

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transpiration and stomatal density and its correlation with atmospheric CO_2 concentration. These interrelationships will be considered in more detail, including a brief description of mechanistic modelling approaches which allow for evaluating putative functional hypotheses (Jordan, 2011). An important aspect is that a trait can be influenced by more than one environmental parameter, making it difficult to extract single climate signals. An example is the possible effect of CO_2 on leaf size, via its effect on stomatal conductance and — therefore — evaporative cooling. The last part of this contribution is dedicated to exploring this interference, as an exemplary study of how the interaction of different parameters could be unravelled by a thorough ecophysiological analysis.

It should be emphasized that this contribution focuses on angiosperms, because many studies are based on angiosperm leaves which show particularly strong and manifold responses to climate. After their appearance and diversification, angiosperms had a substantial influence on global ecology, with their leaves playing a major role (Boyce et al., 2009; Boyce and Lee, 2011; Boyce and Zwieniecki, 2012). Although the majority of studies dedicated to relationships between environment and leaf traits focus on angiosperms, there are also data available which show that various trends found for angiosperm leaves are also valid for other plant groups, such as ferns (Karst and Lechowicz, 2007; Sessa and Givnish, 2014).

2. Macromorphological leaf traits as source for palaeoclimate reconstruction

Probably the most popular — and historical — leaf trait-based indicator of climate is the leaf margin. The approach is usually termed Leaf Margin Analysis (LMA) (Wilf, 1997). Globally, the proportion of taxa showing toothed leaf margins is negatively correlated with mean annual temperature (MAT) (Bailey and Sinnott, 1916; Royer et al., 2012). There is much discussion on the functional background of this climate-dependent trait. It was suggested that marginal teeth — which are often able to act as hydathodes — allow for pressure release during spring root pressure to avoid mesophyll flooding (Feild et al., 2005). According to another hypothesis, toothed margins allow for early maturation of leaf mesophyll at the tip regions and therefore for an early start of photosynthesis at these spots during springtime (Baker-Brosh and Peet, 1997). This hypothesis is supported by the finding that tooth area increases with decreasing MAT (Peppe et al., 2011). However, not all taxa featuring toothed leaf margins show early photosynthesis at their marginal teeth (Baker-Brosh and Peet, 1997), and there are also other explanations for the negative correlation between frequency of taxa with toothed margins and MAT (Edwards et al., 2016; Givnish, 1979; Givnish and Kriebel, 2017).

The occurrence of taxa with toothed leaf margins in a flora has a substantial phylogenetic background. Shifts in proportions of taxa with entire or toothed margins are largely due to species migration by which toothed (mostly deciduous) and untoothed (mostly evergreen) taxa are exchanged against one another (Hinojosa et al., 2011; Little et al., 2010), making biogeography an important aspect in global distributions of toothed vs. untoothed plant groups. This means that there is no globally valid calibration possible since biogeographical history and limitations (such as migration barriers) substantially influence the final frequency of taxa with and without toothed margins. Calibration equations which allow for calculating MAT from extant data sets are therefore regionally limited, and various site-related data sets exist so far (Greenwood et al., 2004; Peppe et al., 2011).

Besides the leaf margin, there are other macroscopic leaf traits which show correlations with environmental factors. CLAMP (Climate Leaf Analysis Multivariate Program) is a multivariate approach based on various (currently 31) leaf traits, such as shape of the leaf lamina or the leaf apex, presence of a drip tip or ratio between leaf length and width. The various correlations of these traits with climate factors are then used for a statistical multivariate approach which returns a number of environmental parameters (Spicer et al., 2009; Wolfe, 1993; Wolfe and Spicer, 1999; Yang et al., 2015, see Kunzmann et al., in this volume, for an example of applying LMA and CLAMP to a fossil assemblage). There are recent efforts for further advanced and sophisticated approaches to calculate climate parameters from leaf traits (Li et al., 2016). These approaches, however, seek not to explain or include possible functional backgrounds of trait–climate relationships. Rather, the observed positive or negative correlations of traits with climate are used in a purely empirical statistical way. It should also be emphasized that neither LMA nor CLAMP requires taxonomic identification of fossil leaves. Both methods can be applied with the “morphotype” concept which is based on characterizing components of a fossil flora by their morphological traits (DiMichele, 1983; Johnson, 1989). This allows for including and analyzing fossils for which no clear taxonomic affiliation to modern taxa is available.

LMA uses categorical data (presence/absence of teeth at the margin) and CLAMP is also mainly based on the categorical data type. Recently, the advantages of continuous leaf traits were put forward (Huff et al., 2003; Royer et al., 2005). A substantial amount of information can be conveyed by quantitative leaf shape parameters, such as roundness or the area covered by marginal teeth (Peppe et al., 2011).

It should be emphasized that biological palaeoclimate proxies (= indirect indicators providing approximate values for the parameter of interest), such as traits of fossil plant remains, come with a certain error margin caused by various reasons. One reason for possible bias is that taphonomic processes can distort the composition of the original flora in a fossil assemblage (Astorga et al., 2016; Campbell, 1999; Ferguson, 1985, 2005; Gastaldo et al., 1996; Greenwood, 2005; Kennedy et al., 2014; Spicer et al., 2011; Steart et al., 2002). Another basic aspect is that a rich assemblage of well-preserved plant fossils is usually dependent on the presence of a water body providing conditions which delay or prevent decay. Many fossil localities thus represent habitats with a high groundwater table, such as riparian systems or swamps in which water supply of the local vegetation is less dependent on precipitation. This is one of the reasons for the notorious difficulty to approximate precipitation on the basis of fossil plants.

Another plant-based method is the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997) (for a recent discussion and state-of-the-art representation see Utescher et al., 2014), whose operational principle is analogous to the Climate Envelope concept: climate reconstruction is based on the realized abiotic environmental niches of the nearest living relatives (NLR) of the considered fossil taxa. Maximum and minimum values of various climate parameters are derived which accommodate the environmental demands of (ideally) all NLRs. Technically, this corresponds to that interval which provides the overlapping region for the climate ranges of the NLRs. In contrast to leaf-trait based methods such as CLAMP and LMA, the CA requires reliable taxonomic identification of the fossil plants, otherwise it would be impossible to recognize NLRs. Furthermore, CA can be applied to all kinds of fossil plant parts, such as wood or pollen, and not just leaves.

How is the performance of leaf-based palaeoclimate reconstruction, compared with other approaches? Quite often, LMA, CLAMP and CA show similar trends, but differences with respect to the absolute values are quite common. For example, evaluation of plant-based palaeoclimate data for an extended stratigraphic range, from the Eocene to the Pleistocene, for the Bohemian Massif (Czech Republic) and adjacent fossil sites in Germany reveals, firstly, that the CA returns a much more equable MAT than LMA or CLAMP, and, secondly, that MAT calculated by leaf-based methods is often several degrees below the CA-derived value (Teodoridis and Kvaček, 2015).

In the case of the CA, the necessity to reliably identify the fossil taxon as well as its correct NLR is often a formidable task (Utescher et al., 2014). However, even if taxonomic identification is correct, there may be substantial differences between the fossil taxon and its extant counterpart (Jordan, 2011). The frequent occurrence of “outliers” which are taxa not fitting into a climate interval enclosing all species, or

even the impossibility to identify such an interval may be due to different climate demands of fossil and extant representative (Utescher et al., 2014). Another problem is represented by the circumstance that combinations of environmental parameters may have occurred in the past which do no longer exist today ("non-analogue climate", see also Section 4.2) (Williams and Jackson, 2007).

Apart from problems which are specific to plant-based proxies, discussing and evaluating climate and climate-dependency of plant traits on the basis of those environmental parameters which were obtained by exactly these traits carries the danger of a circular argument when no other independent evidence for the environment exists. It is generally advantageous to combine different proxies, allowing for comparison between palaeoclimate information derived by plants and those derived by other methods (Jordan, 2011). For example, magnitude of MAT and minimum annual temperature can be approximated by presence of certain animals, such as crocodiles (Markwick, 1998). Other methods are based on isotope composition of animal remains, such as teeth (Kohn and Cerling, 2002; Tütken and Absolon, 2015). For example, palaeotemperature reconstruction of the Messel pith based on $\delta^{18}O$ from enamel obtained from *Propalaeotherium* (a fossil hippomorph) teeth coincides satisfactorily with temperature values derived by using plant fossils (Grein et al., 2011). However, it is often not possible in practice to combine different proxies, because fossil sites frequently do not provide different types of fossil organisms or other material suitable for environmental reconstruction.

3. Fossil leaf economics

As noted above, the functional aspects of many leaf traits whose correlations with environmental parameters are used for palaeoclimate research are unknown or under debate. Furthermore, fossil leaf traits appear to be restricted to morphological traits, seemingly the only kind of trait accessible from fossil material. A functional leaf trait of special interest in recent research is leaf mass per area, LM_{area}, the dry weight of a leaf related to its area, also expressed as its reciprocal, specific leaf area (SLA). LM_{area} correlates with life life span (LLS) and mass-based photosynthesis and is central for explaining leaf function with respect to leaf economics (Reich, 2014; Reich et al., 1999; Wright et al., 2005, 2004). Although it is naturally impossible to directly obtain the weight of a fossil leaf, a method for indirect approximation of LM_{area} from fossil leaves was introduced (Royer et al., 2007). This method is based on mechanical considerations, and approximates LM_{area} from petiole width and lamina area of the fossil leaf specimen on the basis of a quite large calibration set obtained from extant leaves.

LLS is positively correlated with length of the growing season (Givnish, 2002). Due to the relationship between LLS and LM_{area}, the latter parameter could therefore potentially deliver growing season length, thereby complementing other palaeoclimate proxies. For example, LM_{area} data for various fossil assemblages from Central Europe from the Paleocene to the Oligocene confirm general palaeoclimate results indicating warm and equable climate during the Eocene (Figs. 1 and 2). However, mean LM_{area} in a local vegetation as well as LLS are affected also by other environmental factors. Particularly, LM_{area} shows a negative correlation with soil nutrients (McDonald et al., 2003) and increases also with decreasing precipitation (Wright et al., 2005) (for an example of the impact of nutrient availability on plant traits, see Diéme et al., this volume). Particularly availability of soil nutrients is currently not accessible for past habitats (apart from exceptional settings like peat; Sluiter et al., 2017), a circumstance which adds to the uncertainties of plant-based climate reconstruction. Despite these circumstances, fossil LM_{area} data can potentially provide palaeoclimate reconstruction data and contribute basic information on ecophysiological features of fossil plants (Roth-Nebelsick et al., 2017; Royer et al., 2007).

Another parameter which may influence LM_{area} is atmospheric CO_2 concentration (C_a). One line of reasoning is that thin and delicate leaves, thereby tending to a low LM_{area}, should be able to cope better with low CO_2 (Loreto et al., 1992; Medlyn et al., 2011). More robust and dense leaves showing a higher LM_{area} would particularly benefit from high CO_2 (McElwain et al., 2016; Niinemets et al., 2011). This differential effect of CO_2 on the LM_{area} spectrum is caused by differences in leaf internal conductance: high LM_{area} leaves tend to a lower leaf internal conductance for CO_2 than low LM_{area} leaves, and therefore the latter can cope better with low atmospheric CO_2 whereas leaf internal CO_2 transport is promoted for robust and thick leaves under elevated CO_2. This would possibly lead to a CO_2-dependent shift in distribution and frequency of deciduous/evergreen taxa.

Additionally, CO_2 (and various other environmental factors) may directly influence LM_{area} in individual plants via plasticity (Poorter et al., 2009). When exposed to different levels of CO_2, LM_{area} is slightly negatively correlated with CO_2 (Ainsworth and Rogers, 2007; Poorter et al., 2009; Temme et al., 2015). Higher LMA_{area} under elevated C_a is, however, not necessarily caused by structural leaf changes, but can also be due to a higher amount of nonstructural carbohydrates (such as starch or soluble sugars) and therefore reflect changes in the carbohydrate source–sink ratio, such as increased photosynthesis (Poorter et al., 2009).

LMA_{area} is not the only trait which is influenced by CO_2. Since CO_2 is the substrate of photosynthesis, and CO_2 uptake and its fixation is the central element of leaf function, changing CO_2 levels are expected to widely affect leaf ecophysiology and therefore leaf traits. Atmospheric CO_2 changed profoundly during Earth's history, with strong variations throughout the Cenozoic, the post-Cretaceous time period which shaped recent biomes and ecosystems (Beerling and Royer, 2011). In the following sections, basic aspects of relationships between leaf traits of fossil plants and CO_2 will be considered.

4. Leaf traits and CO_2

4.1. Stomata respond to CO_2 — and can be used as proxy data for the past

During the last years, a large wealth of data on the response of plant gas exchange to CO_2 was collected, mostly with respect to elevated levels, such as targeted by the FACE (Free Air Carbon dioxide Enrichment) campaign (Ainsworth and Long, 2005; Battipaglia et al., 2013; Norby et al., 2016; Norby and Zak, 2011). Various studies considered also plant responses to subambient CO_2 (Bunce, 2007; Gerhart and Ward, 2010; Pinto et al., 2014; Temme et al., 2013). As one general result, stomatal conductance, g, is negatively correlated with CO_2, with plants adapting stomatal opening to atmospheric availability of CO_2. The negative g–CO_2 relationship represents one of the various responses of the stomatal control system to environmental parameters, but a negative correlation between stomatal density (SD or ν) and CO_2 was also observed, for herbarium material (Miller-Rushing et al., 2009; Peñuelas and Matamala, 1990; Woodward, 1987) as well as experimentally (Beerling et al., 1998; Haworth et al., 2011; Hincke et al., 2016; Kürschner, 1996; Wagner et al., 1996). Contrary to g, stomatal density represents a morphological trait and can as such be determined from fossil material, if the cuticle of a fossil leaf is properly preserved (Fig. 3). Therefore, quite soon after the publication of Woodward (1987), SD advanced to a wide-spread tool for palaeoatmospheric CO_2 reconstruction. In the following, atmospheric CO_2 concentration will be termed C_a.

As the SD–C_a relationship is species-dependent, the original concept was to identify extant species whose existence extended to the time period of interest and to erect calibration curves of their SD–C_a relationship, either by herbarium material or from experiments. These calibration curves are then used to calculate C_a from fossil SD data (or from stomatal index data representing the ratio between epidermal cell density and stomata density) (Kürschner et al., 1998; Poole and Kürschner, 1999). Naturally, this strategy becomes increasingly difficult to pursue with increasing stratigraphic age. Plant taxa of the

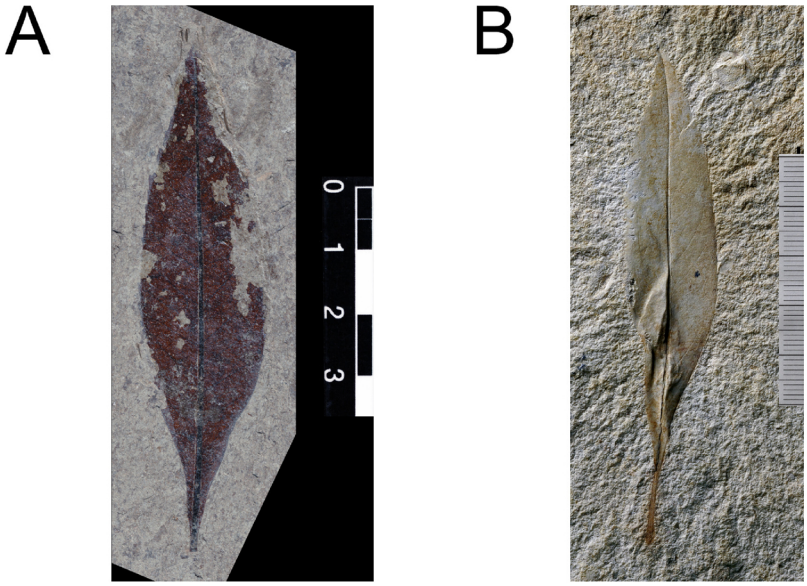

Fig. 1. Two leaves of *Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček, from two different localities, as an example for fossil leaf material which allowed for determination of LM_{area}. (A) *P. neptuni* from the fossil site Rauenberg (State Museum of Natural History Stuttgart, SMNS P 1953/36) (Kovar-Eder, 2016). Stratigraphic age: Oligocene, Rupelian, about 32 to 29.6 million years old. (B) *P. neptuni* from the fossil site Kučlín, Czech Republic. Stratigraphic age: Eocene, Bartonian, about 39.2 to 37.4 million years old (National Museum Prague, NMP G 09792) (Teodoridis and Kvaček, 2015).

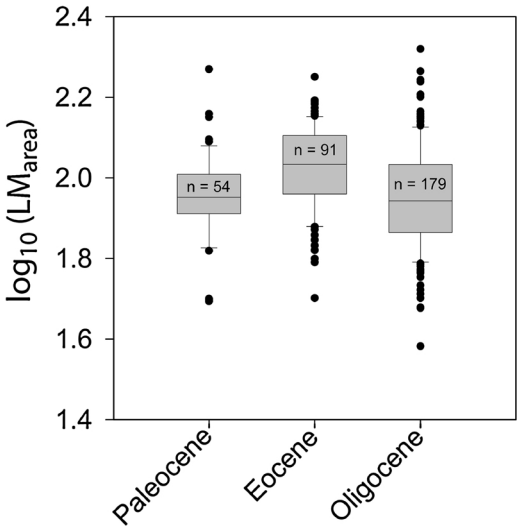

Fig. 2. Data for mean LM_{area} of various fossil assemblages from Central Europe, from the Paleocene, Eocene and Oligocene. The box plots span the 50% interquartile. The lines within the boxes indicate the median values. The "whiskers" mark the highest and lowest values. Outliers are drawn as filled circles. Differences are statistically significant (for more detail, see Traiser et al. (2018)). Note: expression $\log_{10}(LM_{area})$ (along ordinate axis) is to be understood as the common logarithm of the numerical value of LM_{area}, provided LM_{area} is given in units of g/m^2.

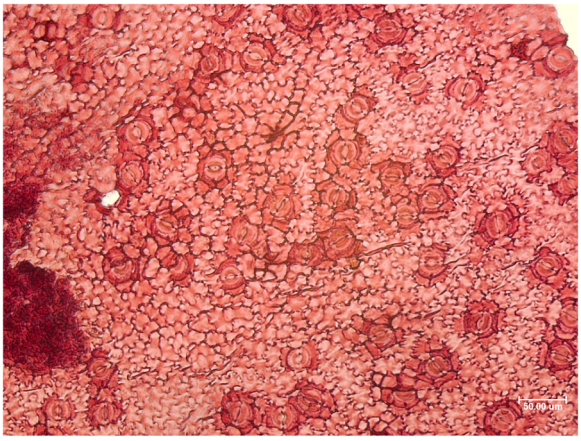

Fig. 3. Abaxial cuticle of the fossil angiosperm taxon *Rhodomyrtophyllum reticulosum* from the Messel pit, about 48 million years old (Ypresian, Eocene) (Courtesy Michaela Grein, Übersee-Museum Bremen, Germany). Bar: 50 µm.

Quaternary, for example, are almost identical to recent taxa, offering excellent opportunities to study C_a from fossil material (Beerling and Rundgren, 2000; Rundgren and Beerling, 1999; Rundgren and Björck, 2003; Steinthorsdottir et al., 2013; Wagner et al., 2004). For time periods older than the Miocene, suitable species become increasingly scarce, leaving some few taxa with a long history ("living fossils").

Another strategy is to use plant gas exchange modelling as basis for calculating C_a from fossil stomatal data. This opens up possibilities for an ecophysiological model framework as basis for deriving palaeoclimate from proxy data, and will be presented in the following in more detail — although briefly — as an exemplary case. All different modelling approaches exploit two relations. The first one, Fick's Law of diffusion, states that the flux of CO_2 molecules into leaves is driven by their concentration difference between atmosphere (C_a) and leaf interior (C_i). Under stationary conditions, the net flux of CO_2–molecules into the plant is entirely processed by photosynthesis, and assimilation rate A is related to leaf conductance g via

$$A = g\,(C_a - C_i) \tag{1}$$

Furthermore, the Farquhar model of C_3–plant photosynthesis (Farquhar et al., 1980) postulates a dependence of A on C_i and on biochemical parameters

$$A = q\,\frac{C_i - \Gamma}{C_i + K} - R_d \tag{2}$$

with q: carboxylation limited by RubisCO or RuBP, K: parameter containing Michaelis–Menten constants of carboxylation and oxygenation, Γ: CO_2 compensation point, and R_d: mitochondrial respiration rate in the daylight as biochemical parameters of photosynthesis (Farquhar et al., 1980; Konrad et al., 2008). These parameters depend on temperature (Bernacchi et al., 2003; Konrad et al., 2008).

The diffusion law provides also a relation between stomatal conductance and leaf anatomy (Parlange and Waggoner, 1970; Konrad et al., 2008),

$$g = \frac{\nu a_{st} D_{CO_2}}{\left[d_{bl} + d_{as}\frac{\tau_{as}^2}{n_{as}}\right]\nu a_{st} + d_{st}} \tag{3}$$

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d_{as}, τ_{as}, n_{as} are thickness, tortuosity, and porosity of the assimilation layer, a_{st}, d_{st} are cross-sectional area (parallel to the leaf surface) and depth of the stoma, and ν is the stomatal density. A laminar boundary layer of air develops around a leaf whose thickness depends on leaf size l and wind speed v_{wind}, approximately according to $d_{bl} \approx 4 \times 10^{-3}\,\mathrm{m}/\sqrt{s}\sqrt{\frac{l}{v_{\mathrm{wind}}}}$.

The basic model idea amounts to deriving — in a first step — from (1) and (2) a relation between g and C_a and to use this result in (3) which can then be solved for C_a. Assuming that the photosynthesis parameters q, K, Γ and R_d are known from extant relatives, the two equations (1) and (2) contain four unknowns, g, C_a, A and C_i. Thus, a third relation is required in order to extract the desired relation between g and C_a.

At this point, the model approaches diverge somewhat:

(i) The optimization models include the dependency of stomatal aperture on environmental parameters, particularly humidity and temperature and postulate optimized water use (Konrad et al., 2008). The strategy of plants to gain a maximum of carbon with a given amount of available water (Berninger et al., 1996; Cowan, 1977) can be translated into the mathematical language of optimization principles. Several of them were successfully applied on various occasions (Aalto et al., 2002; Berninger et al., 1996; Buckley and Schymanski, 2013; De Boer et al., 2011; Katul et al., 2010; Way et al., 2011). The approach of Konrad et al. (2008) employs a full optimization model and is quite complex, requiring besides information for temperature and humidity also determination of a parameter λ which quantifies in a sense the "cost of water" and is constrained by the ratio C_i/C_a. (Notice that our definition of λ is the inverse of the definition used in Cowan and Farquhar, 1977.)

(ii) Most of the other models restrict their model dynamics to carbon balance. They obtain the missing information on stomatal conductance from determining C_i/C_a, based on the well-known fact that both diffusion and photosynthesis discriminate the ^{13}C isotope against the ^{12}C isotope. Exploiting this fact, it is possible to calculate the ratio

$$\kappa = \frac{C_i}{C_a} \tag{4}$$

from $\delta^{13}C$ data from fossilized leaves (Beerling, 1994; Diefendorf et al., 2010; Farquhar et al., 1982; Grein et al., 2010).

Pursuing the second approach, we combine Eqs. (1), (2) and (4), and arrive at (Konrad et al., 2017)

$$g = \frac{q(\kappa C_a - \Gamma)}{(1-\kappa)C_a(\kappa C_a + K)} - \frac{R_d(\kappa C_a + K)}{(1-\kappa)C_a} \tag{5}$$

the right hand side of which contains — apart from the photosynthesis parameters (obtainable from living relatives) and κ (obtainable from the fossil leaves) — only C_a. Expression (3) connects g with leaf anatomy (obtainable from the fossil leaf) and the coefficient of diffusion D_{CO_2}. Equating expressions (3) and (5) results in a quadratic equation for the atmospheric CO_2 concentration C_a under which the fossilized leaf had grown.

Being not based on calibration curves from extant species, gas exchange model approaches are also applied to extinct fossil taxa (Franks et al., 2014; Grein et al., 2011). Furthermore, in contrast to calibration methods, gas exchange models also include stomatal parameters other than SD, namely stomatal pore size and depth and therefore consider all traits which influence stomatal conductance. In fact, stomatal pore length may change over time within a taxon which can substantially alter the relationship between C_a, g and gas exchange (García-Amorena et al., 2006; Miller-Rushing et al., 2009; Roth-Nebelsick et al., 2012; Wagner et al., 1996).

Results of CO_2 reconstruction with fossil stomata are quite consistent when compared to CO_2 values from ice cores (Franks et al., 2014). However, ice core data are only available for about one million years into the past (Fischer et al., 2013), and the error margin of stomata-based CO_2 reconstruction will increase when going further back in time, due to higher uncertainty of photosynthesis parameters as well as environmental parameters. A comparison of stomata-derived CO_2 with results of other proxy sources (such as Boron isotopes or alkenon-derived $\delta^{13}C$ from marine plankton) reveals various consistent trends (Beerling and Royer, 2011). However, there are also inconsistencies, particularly during a time of strong climate change, namely the Eocene–Oligocene when global cooling terminated the ice-free hothouse conditions, marked by the Oi-1 glaciation event (Coxall and Wilson, 2011; Coxall et al., 2005). There is various evidence for high CO_2 during the Eocene, with a more or less continuous decline towards the Oligocene. A decrease in C_a would thus accompany global cooling (Royer et al., 2012). Stomata-based results for the Eocene are often substantially lower and at odds with other proxies (Anagnostou et al., 2016; Maxbauer et al., 2014; Steinthorsdottir et al., 2016), despite the circumstance that various Eocene C_a data originally reported as extremely high were meanwhile revised and became more moderate (Breecker et al., 2009; Jagniecki et al., 2015). These disparities among CO_2 proxies are currently not resolved (Cui and Schubert, 2017; Royer et al., 2014).

In the case of stomata-based proxies, one possible source of error is the increasing insensitivity of gas exchange to CO_2, due to the non-linear response of stomatal conductance g and assimilation rate A to C_a (see Fig. 4). At low or subambient CO_2, g (see Fig. 4a) as well as A (see Fig. 4b) respond strongly and roughly linearly to changing C_a levels (Franks et al., 2013, 2012; Temme et al., 2013) (see Fig. 4). With elevated C_a, usually above about 400–500 μ mol mol^{-1} (depending on temperature), the response increasingly levels off: A approaches saturation (the saturation value depends on temperature), a consequence of Eq. (2), the Farquhar model of C_3-plant photosynthesis, and equation (4), expressing proportionality of the CO_2-concentrations inside and outside of the plant. g, however, becomes according to Eq. (5) smaller under further increasing C_a (Franks et al., 2013, 2012; Konrad et al., 2008). SD and E, which are connected with g via Eqs. (3) and (7), follow this trend (see Fig. 4c). Therefore, adding a certain increment of CO_2 to an already high C_a leads to a very small (decreasing) step on the SD-axis which is statistically difficult to ascertain, particularly when the naturally high scatter of SD data is considered. Despite these problems it is, however, principally possible to reconstruct elevated C_a from stomatal data (Grein et al., 2011; Tesfamichael et al., 2017).

Gas exchange approaches offer the possibility of evaluating the error margin of CO_2 reconstructed with fossil stomatal data by varying the input parameters over their whole range of (statistical) uncertainty (Konrad et al., 2008). Furthermore, it is possible by systematic parameter variation to identify parameters which exert the highest influence ("critical parameters") on the results. In this manner, it can be shown that the biochemical parameter q (carboxylation limited by Rubisco or RuBP) represents a critical parameter (Konrad et al., 2008). Biochemical parameters are the only ones which have to be borrowed from extant plants, introducing a basic source of error for CO_2 reconstructed from fossil stomata. This error introduced by photosynthesis parameter is exacerbated by the circumstance that q itself is affected by CO_2: q tends to decrease somewhat when plants are exposed experimentally to elevated C_a (Ainsworth and Rogers, 2007), whereas it increases under subambient CO_2 (Pinto et al., 2014). Adaption of the photosynthesis system to C_a by this plastic response can be connected to nitrogen content of the plant: it tends to be higher under subambient conditions compared to control groups (Pinto et al., 2014). Probably, q shifted also during land plant evolution, according to changing C_a levels (Franks and Beerling, 2009). The possible sensitivity of q to C_a increases the error margin when determining C_a from fossil stomata. All these uncertainties also affect calibration-based approaches. This

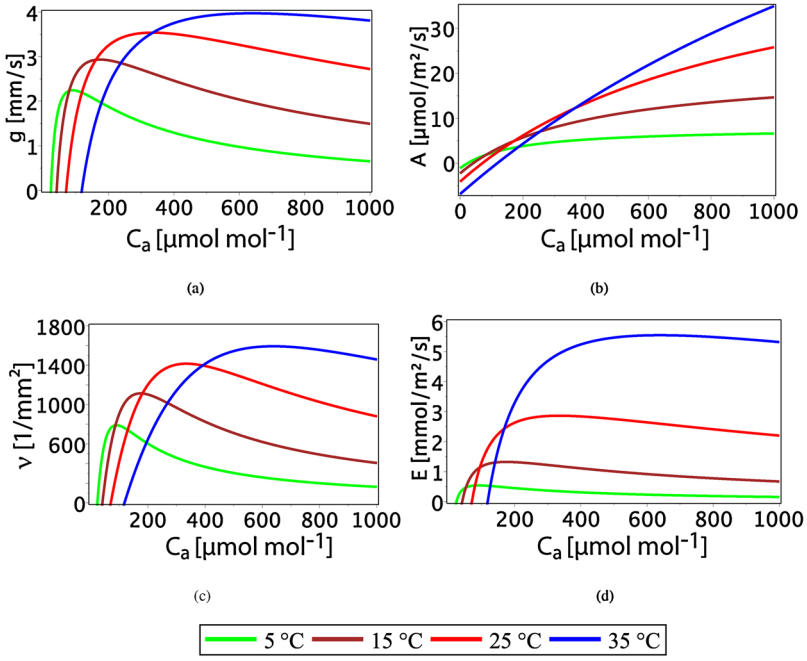

Fig. 4. Results obtained from applying the model (expressions (1) through (5) and (7)) to *Quercus petraea*: (a) leaf conductance g, (b) assimilation rate A, (c) stomatal density ν and (d) transpiration rate E as a function of atmospheric CO_2 for several values of atmospheric temperature T_a. Relative atmospheric humidity is $w_{rel} = 0.6$, $\kappa = 0.77$, leaf length $l = 3$ cm, wind speed $v_{wind} = 1$ m/s. At high C_a levels, the stomatal density response $\nu(C_a)$ increasingly levels off, following the basic response of g to increasing C_a.

"ecophysiological" error margin is, however, "hidden" for calibration–based methods.

4.2. Interference of CO_2 with other environmental parameters and the problem of non-analogue climates

Response of SD and g to C_a is part of the far-reaching influence of CO_2 on plant physiology and ecology, and can interfere with responses to other environmental parameters. During glacials, C_a amounted to about 180 µ mol mol^{-1}, lowering WUE considerably, as can also be recognized by C_i/C_a data of fossil plant material derived from carbon isotopes (Gerhart et al., 2012). Low C_a conditions can therefore mimic low-humidity conditions. Conversely, elevated C_a can mitigate low water availability: Plants may therefore need less water under elevated C_a for the same or a higher amount of carbon harvest. The apparent influence of C_a on water demand has various consequences, depending on vegetation type and environmental conditions. For example, a temperate and mesic forest exposed to elevated C_a may need less water, due to lower g, leading to a higher soil water content (Bader et al., 2013). At warm and drier sites, plants can produce more foliage cover with rising C_a, compared to pre-industrial C_a (Donohue et al., 2013). In fact, the recent anthropogenic rise in C_a appears to affect vegetation cover in various ways, promoting LAI or "greening" of landscapes beyond what is expected from local precipitation, as indicated by remote sensing and other data (Ukkola et al., 2016; Zhu et al., 2016). Many of these developments can be explained by "CO_2 fertilization" which is the enhancement of photosynthesis by elevated C_a, as is widely demonstrated by experiments (Ainsworth and Rogers, 2007).

Consequently, the taxon-specific humidity threshold limiting the ecological niche can be shifted by C_a. Possible impact of CO_2 on species-specific environmental demands means that current abiotic climate envelope data may not hold true for the past (or the future). Combination of CO_2 values different to extant levels with other environmental parameters leads to "non-analogue climates", meaning conditions for which no extant counterpart exists (Bennett and Willis, 2000; Jackson and Blois, 2015; Williams and Jackson, 2007). In fact, there is evidence for shifts in niche demands for past vegetation, with species distributions being incongruent with palaeoenvironmental data (Worth et al., 2014). Non-analogue environments can also lead to species compositions within a flora which cannot be found today (Jackson and Williams, 2004; Williams and Jackson, 2007).

Considering, however, the effect of C_a on gas exchange, the function $g(C_a)$ is most sensitive below ambient C_a (see Fig. 4). It may thus be assumed that for time periods with elevated C_a changes in CO_2 do not affect water demand very much. With respect to future C_a rise, it might be the case that we have already passed the period in which C_a acts strongest on plant physiology and ecology.

The influence of C_a on transpiration affects leaf temperature, because evaporation consumes heat. Leaf temperature, in turn, depends also on leaf size, a character which is sensitive to various environmental parameters and therefore included as "proxy trait" in, for instance, CLAMP. The interrelationships between transpiration, evaporational cooling, CO_2, leaf size and temperature represent an excellent example of (assumed) intertwined environmental effects which are suitable to be unraveled by a mechanistic analysis. In the following, these interrelationships will be evaluated on a physical–physiological basis to arrive at a first estimation of the putative bias which CO_2 can possibly exert on the correlations between leaf size and other environmental parameters.

4.3. Does CO_2 affect leaf temperature and leaf size?

4.3.1. Large leaves vs. small leaves

Species showing large leaves are preferentially found in humid habitats which also show sufficient availability of nutrients (Givnish, 1984; McDonald et al., 2003; Nicotra et al., 2011; Peppe et al., 2011; Wright et al., 2017). Also, the xylem of large-leaved taxa is quite vulnerable to cavitation, and therefore not able to cope with low humidity (Schreiber et al., 2016). In fact, leaf size is a CLAMP parameter and is occasionally also used alone as a proxy for palaeoprecipitation (Wilf

et al., 1998). The positive correlation of leaf size with humidity is commonly explained on the basis of boundary layer conductance. Larger objects show — all other factors like wind velocity and surface topography being equal — a thicker boundary layer and therefore a lower boundary layer conductance than smaller objects (Schuepp, 1993). Boundary layer conductance is a component of the total leaf conductance, therefore also affecting gas exchange, but usually to a minor (or even negligible) degree (Schuepp, 1993). For leaf heat transfer, however, boundary layer conductance is crucial. With increasing boundary layer thickness resistance to heat dissipation rises, and large leaves will tend to higher leaf temperatures than smaller leaves under identical conditions.

Small leaves should therefore be particularly suitable in hot and dry environments because no transpiration is required to prevent heat damage and/or depression of photosynthesis due to excessively high leaf temperatures (Yates et al., 2010). Preventing heat damage is, however, not the only factor which couples rising leaf temperature to rising water demand. With a given g, elevated leaf temperature promotes leaf-internal evaporation and, therefore, higher transpiration rates (Jones, 1992). The relationship between boundary layer thickness, leaf size and leaf temperature can be modulated by leaf shape, for example by making the leaf longer and narrower (Monteith and Unsworth, 2008; Schuepp, 1993). Also, the boundary layer thickness of lobed leaves is substantially decreased and more independent of wind direction as compared to unlobed leaves (Roth-Nebelsick, 2001; Vogel, 2009).

It is difficult to exactly predict leaf temperature for real leaves under natural conditions. The well-known approximative equations for boundary layer thickness, such as provided in Nobel (2009), have their origin in engineering science and focus on artificial flat or round objects with a smooth surface. Moreover, experimental studies often employ wind channel environments with laminar inflow regime while natural winds show a high turbulence intensity. Additionally, various leaf surface structures, such as trichome covers, are capable of an enhanced infrared reflectivity and affect also the airflow patterns around leaves. Thus, strongly varying wind conditions and complex topographic leaf surface profiles substantially affect local leaf temperature and its distribution in real leaves (Leigh et al., 2016; Saudreau et al., 2017; Wigley and Clark, 1974). Although natural leaf temperature profiles are much more complex than in approximative models, intensified convective cooling will — in contrast to evaporative cooling — be principally advantageous under conditions of limited water availability because it curbs transpirational water loss. Growing smaller and/or stronger dissected leaves represents thus a suitable strategy in warm and dry environments. Leigh et al. (2016) showed that usually leaf temperature exceeds air temperature, that this effect is positively correlated with effective leaf width, and that leaf shapes promoting convective leaf heat transfer might be favoured in open habitats, as was recently found for Proteaceae (Onstein et al., 2016).

Elevated C_a may indirectly act upon leaf temperature, via suppressing evaporative cooling by transpiration, leading to “warmer leaves”. The consequences of high CO_2 for leaf temperature regulation were discussed for future climate scenarios under the current anthropogenic rise of CO_2, proposing the possibility of rising mean leaf temperatures (Cernusak et al., 2013; Doughty and Goulden, 2008; Voelker et al., 2016). Also, the impact of high C_a on leaf temperature was discussed as a factor for leaf evolution for climates of the past (Lee et al., 2015; Beerling and Berner, 2005; McElwain et al., 1999). It was even proposed that high C_a levels which prevailed during early land plant evolution were responsible for the considerable delay in the development of macrophyllous leaves, due to the circumstance that a very low stomatal conductance was sufficient at that time to fuel photosynthesis, and the entire structure of early land plants was accordingly adapted, showing low stomatal density and finely divided terminal parts of the branching stems (see Fig. 5; Raven and Edwards, 2014; Beerling et al., 2001).

Does this mean that plants with large leaves, as components of a vegetation which is adapted to low C_a, will indeed run into problems under the current rising C_a and global temperature?

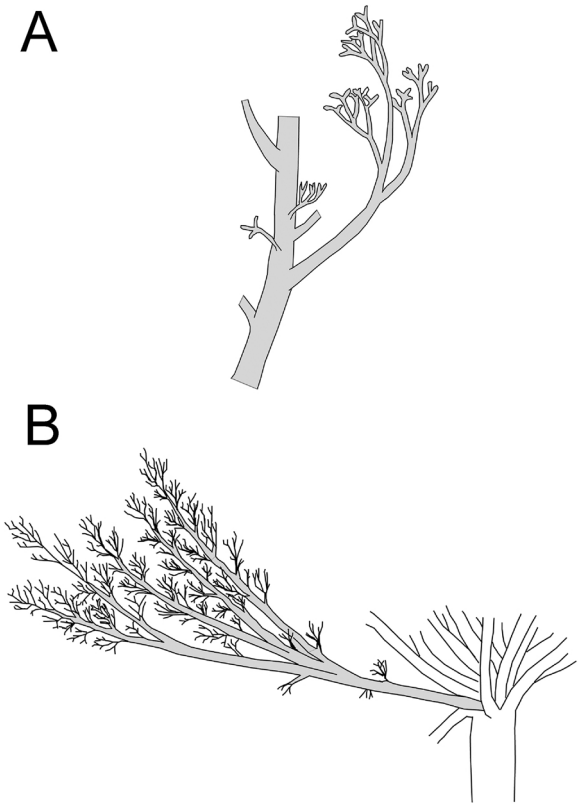

Fig. 5. Examples for branching axis systems of Devonian plants without webbed leaves. (A) A part of the branching system of *Psilophyton*, terminating with isotomous ultimate units (redrawn from Banks et al., 1975). (B) A lateral branch of *Pseudosporochnus*, equipped with ultimate appendages (redrawn from Berry and Fairon-Demaret, 2002).

With respect to thermal damage, a value of about 40 °C is quoted as general upper limit for thermostability (Larcher, 2003). However, plants growing in hot and sunny habitats are quite thermostable, and can be able to tolerate leaf temperatures of 50–60 °C (Larcher, 2003). A main concern are extreme events, such as exceptional heat waves which may in fact drive leaf temperature into critical heights (O'sullivan et al., 2017), making convective heat transfer an important issue. Beyond the topic of thermal damage, there is still the issue of higher transpiration rates in “warmer” leaves under a given stomatal conductance and boundary layer, due to rising water vapor content of the leaf internal air. Thus, leaf temperature and transpiration rate are — all other conditions being equal — positively and dynamically coupled. The final effect of elevated C_a on leaf temperature is, however, difficult to predict since higher transpiration rates lead to higher evaporative cooling. In the following chapter, model studies addressing this interrelationship are presented.

4.3.2. Modelling the interaction of CO_2, leaf temperature and leaf size

The simple model introduced in Eqs. (1) to (5) can be expanded to predict leaf temperature T (in addition to leaf conductance g and transpiration rate E) if atmospheric temperature T_a, atmospheric humidity w_a and insolation are given. This is achieved by including leaf energy balance into the already derived system of equations. In the following a brief outline is provided. Conservation of energy under stationary conditions requires

(energy into leaf) = {energy out of leaf}

+ [energy consumed by leaf metabolism]

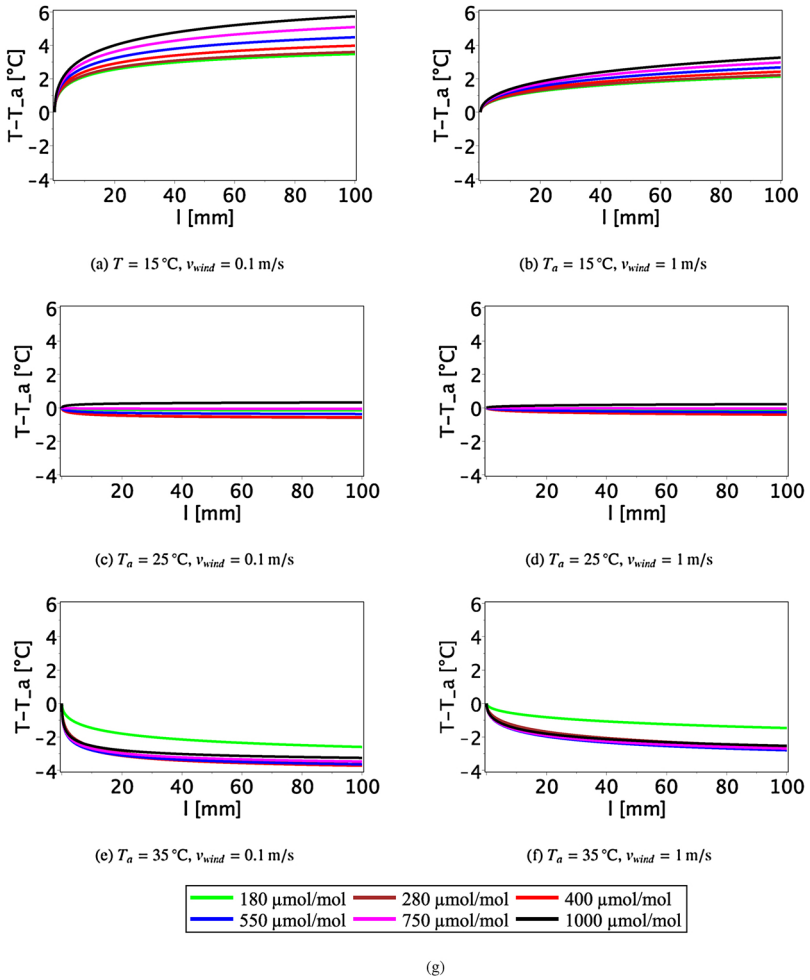
T−T_a [°C]
l [mm]
(a) T = 15 °C, v_{wind} = 0.1 m/s
(b) T_a = 15 °C, v_{wind} = 1 m/s
(c) T_a = 25 °C, v_{wind} = 0.1 m/s
(d) T_a = 25 °C, v_{wind} = 1 m/s
(e) T_a = 35 °C, v_{wind} = 0.1 m/s
(f) T_a = 35 °C, v_{wind} = 1 m/s
180 µmol/mol
280 µmol/mol
400 µmol/mol
550 µmol/mol
750 µmol/mol
1000 µmol/mol
(g)

Fig. 6. Difference between leaf temperature T and atmospheric temperature T_a as a function of leaf length l for several values of atmospheric CO_2 for *Quercus petraea*. The single plots represent different combinations of wind speed v_{wind} and atmospheric temperature T_a. Relative atmospheric humidity is $w_{\mathrm{rel}} = 0.6$ and C_i/C_a ratio is $\kappa = 0.77$, for all cases. The different colours of the curves denote the atmospheric CO_2–concentration.

Since metabolistic processes consume only a very small amount of the leaf energy input, it is justified to simply neglect them. In mathematical terms, leaf energy balance amounts then to (Nobel, 2009):

$$a(1+r)S_c\tau_N^{1/\sin\gamma}\sin\gamma + a_{\mathrm{IR}}\sigma(T_{\mathrm{surr}}^4 + T_{\mathrm{sky}}^4) = 2e_{\mathrm{IR}}T^4 + \frac{2K_{\mathrm{air}}}{d_{\mathrm{bl}}}(T - T_a) + H_{\mathrm{vap}}E(T) \quad (6)$$

The left hand side is the sum of direct solar radiation plus solar radiation reflected by the surroundings (first term) and absorbed infrared radiation emanating from the surroundings and the sky (second term). The right hand side sums three kinds of leaf energy losses: infrared radiation emitted by the leaf (first term), heat conducted through the boundary layer to the open atmosphere (second term) and the loss of latent heat stored in the water vapour which emanates from the leaf interior (third term). The transpiration rate is given by

$$E(T) = \mathrm{ag}(w_{\mathrm{sat}}(T) - w_a) \quad (7)$$

where w_a denotes the (absolute) atmospheric humidity and $a := D_{H_2O}/D_{CO_2}$. The temperature dependence of the saturation concentration of water vapour within the leaf is given by the Clausius–Clapeyron equation, $w_{\mathrm{sat}}(T) = (c_1/T)\mathrm{e}^{-(c_2/T)}$ ($c_1 = 2.035 \times 10^{10}$ mol/m^3 and $c_2 = 5306$, T in Kelvin) (Reif, 1974). Further quantities appearing in (6) are $S_c = 1366$ J/m^2/s (solar constant), $\sigma = 5.67 \times 10^{-8}$ J/m^2/s/K^4 (Stefan–Boltzmann constant), $K_{air} = 2.57 \times 10^{-2}$ J/m/s/K (coefficient of thermal conductivity of air at 20 °C), $H_{vap} = 40.68 \times 10^3$ J/mol (vapourization heat of water), $\gamma \approx 45°$ (angle of sun above horizon), $\tau_N \approx 0.7$ (atmospheric transmittance for moderate clear sky at moderate elevation), $a \approx 0.60$ (absorptance of leaf for global radiation), $r \approx 0.20$ (reflectance of the surroundings for global radiation), $a_{IR} \approx 0.96$ (leaf absorptivity for infrared radiation), $T_{surr} \approx 20$ °C (temperature of the surroundings), $T_{sky} \approx -20$ °C (radiation temperature of the clear sky), $e_{IR} \approx 0.96$ (leaf emissivity for infrared radiation). Several of these quantities vary with the composition of the surrounding vegetation and with climate. The numerical values given represent typical values (for details consult Nobel (2009)).

In the following we present exemplary model results for leaf cooling and heating effects. From Fig. 6 some basic results concerning leaf cooling and heating and the impact of CO_2 on leaf temperature may be derived for *Quercus petraea*:

- Leaf heating takes place for atmospheric temperature $T_a = 15$ °C and cooling for $T_a = 35$ °C. At $T_a = 25$ °C, leaf temperature T is quite similar to T_a.
- The dependence of leaf temperature on C_a is quite weak, and almost non-existent for $T_a = 25$°C. The effect of C_a becomes more pronounced for elevated C_a but is nonetheless weak. Strongest impact of C_a on leaf temperature occurs for $T_a = 15$ °C and elevated C_a.
- Leaf size matters only for leaves which are shorter than roughly 3 cm.
- Dependence of leaf temperature on wind speed is not very strong, but more pronounced for smaller wind speeds.

In summary, the model results indicate that large leaves — as opposed to general expectation — do not heat up under high air temperature, but even cool down. Obviously, the transpirational effect of lower g under elevated C_a is not strong enough to be of relevance for the interconnected processes of evaporation and heat dissipation. Moderate leaf heating occurs for larger leaves under lower air temperatures, as was also proposed by Okajima et al. (2012), but are then easily cooled by moderate wind movements which commonly occur in tree canopies. It should, however, be emphasized that availability of water and therefore transpiration was not restricted. The modelled situation thus applies to a situation of unlimited water supply and therefore unrestricted transpiration. Under these conditions, C_a has no or negligible influence on leaf heat dissipation and does not limit leaf size. The problem of overheating under elevated C_a is apparently of relevance only for habitats or situations of low soil water availability.

5. Summary

There is much current interest in leaf trait–climate correlations, and research which involves extrapolations of these correlations into the past, such as reconstruction of past climates based on leaf traits, or into the future would largely benefit from an improved understanding of functional traits. The circumstance that plant-based proxies for palaeoclimate appear to catch overall trends reasonably well suggests that various responses of leaf traits to environment may be also extrapolated into future climate scenarios. However, some inconsistencies and problems remain. Of special interest are the manifold aspects of the impact of CO_2 on leaf function. Vegetation was repeatedly exposed to changing CO_2 levels which were often combined with changing climate, and both represent important drivers for land plant evolution. The impact of non-analogue climate situations, representing combinations of abiotic environmental parameters which do not exist today and particularly so with subambient or elevated CO_2, on plant function is difficult to predict. As an example, the possible rise of leaf temperature under elevated CO_2 was considered, being expected due to the coupling of transpirational cooling and stomatal conductance. Since transpiration and leaf temperature are dynamically linked, there is, however, no straightforward prediction of leaf heat dissipation under changing CO_2 and a closer analysis based on a model connecting gas exchange and leaf heat transfer indicated in fact that the effect of elevated CO_2 on leaf temperature may be minor, at least when water supply is not limited. Correlations of leaf size with abiotic environmental parameters thus appear to be not — or only moderately — affected by C_a, at least in habitats with sufficient water availability. This example demonstrates that ecophysiological analyses of functional leaf traits can particularly contribute to identifying adaptive features of leaf architecture and to evaluate predictions into the future as well as into the past.

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